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THE VELIGER

Distribution and Diversity Patterns of Australian Pupilloid Land Snails (Mollusca: Pulmonata: Pupillidae, s.l.)

by

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Abstract. Data are presented on the distribution and diversity patterns of 34 native Australian pupilloid land snails. In addition, mention is made of two introduced species. Most Queensland and New South Wales species have not been revised and distributional data for these taxa are sparse. Therefore, they are not included. Eight of the nine genera range outside of Australia. The monotypic *Glyptopupoides* Pilsbry, 1926, is the only restricted endemic. Four of the 34 native species also live in Indonesia or New Guinea.

The south and west coasts of Australia have a limited fauna of three genera and four restricted endemic species each, plus a minor intrusion of *Gastrocopta deserti* Pilsbry, 1917, from the "Red Centre." No pupilloids have been collected in the humid southwestern corner of Western Australia, Tasmania, or most of Victoria. The "Red Centre" has seven species, two with quite restricted ranges, in three genera. One "Red Centre" species, *G. deserti,* has the widest range of any Australian pupilloid, extending from western Queensland to the North West Cape in Western Australia, as far north as the south fringes of the Kimberley, and then south to the Flinders Ranges in South Australia.

The Kimberley in Western Australia and the "Top End" of the Northern Territory have the greatest diversity in both genera and species, with eight genera and 19 species present. Local distribution in this region is rather complex and correlates mainly with moisture regimes.

Patterns of local diversity also are discussed.

INTRODUCTION

As a by-product from extensive field surveys of the camaenid land snails found in the western two-thirds of Australia, collections of the small-sized and much less diverse non-camaenid families have been accumulated. Pupilloid taxa proved to be especially abundant and moderately diverse. Their shells provide a wealth of characters for species delineation. It was thus possible to review the species found in Australia and determine if they have extralimital ranges. In the absence of any contemporary generic or family level phylogenetic hypotheses and anatomical data on the Australian taxa, it proved impossible to expand these studies into reviews of generic affinities or historical biogeography.

The systematic bases for this study are the survey of Australian members of the basically Southeast Asian-Indonesian genus *Glyiotrachela* Tomlin, 1930 (see SOLEM, 1981); a faunal review of pupilloid species from the south

† **Editor's note:** Several weeks before his death on 26 February 1990, Alan Solem mentioned to one of his colleagues at the Field Museum, Vickie Huff, that he was working on "the pupillid range paper" at home and that he had one part to finish before submitting it to *The Veliger.* Regrettably, he did not have the opportunity. Ms. Huff, however, was able to gather all of the previously completed, computer-generated figures and to retrieve the text from Alan's computer. She submitted the posthumous manuscript to *The Veliger* in accordance with Alan's expressed intent; it was evaluated by three reviewers, and accepted for publication. Although we suppose that the manuscript was nearly complete, readers may notice a few places where Alan was likely to have returned to fill in a section or to make a revision. Nevertheless, only minor editorial changes were made in the submitted manuscript in order to preserve, as much as possible, the author's intent. After the initial manuscript submission, Margaret Baker of the Field Museum took over the responsibility of seeing the project through to completion. Without her considerable efforts we would not now have the opportunity to read Alan Solem's last contribution to science. D.W.P.

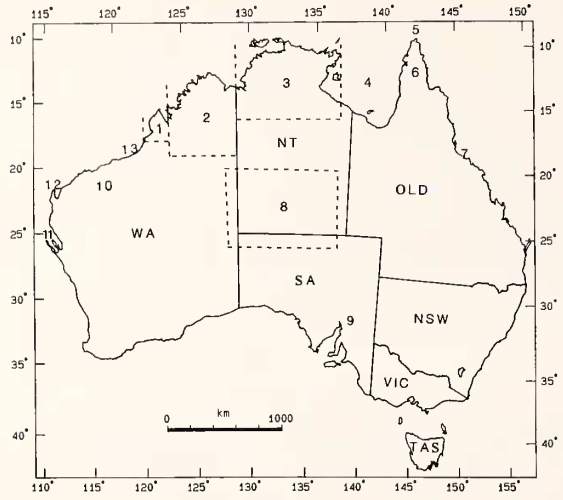

Figure 1

Map of Australia showing approximate outlines of regions discussed in text: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia; 1, Dampierland; 2, Kimberley; 3, "Top End"; 4, Gulf of Carpentaria; 5, Torres Strait; 6, Cape York Peninsula; 7, Townsville, QLD; 8, "Red Centre"; 9, Flinders Ranges; 10, Pilbara; 11, Shark Bay; 12, North West Cape; 13, 80 Mile Beach.

and west coasts of Australia (see SOLEM, 1986); and a monographic review of all non-camaenid land snails from the Kimberley region of Western Australia and all of the Northern Territory (see SOLEM, 1989).

These studies not only greatly extended the known ranges of most taxa and resulted in recognition of several new ones, but permitted preparing the first comprehensive set of distributional maps for any Australian land snail family (Figures 2–32). The patterns of both distribution and diversity were unexpected. The extent to which there are

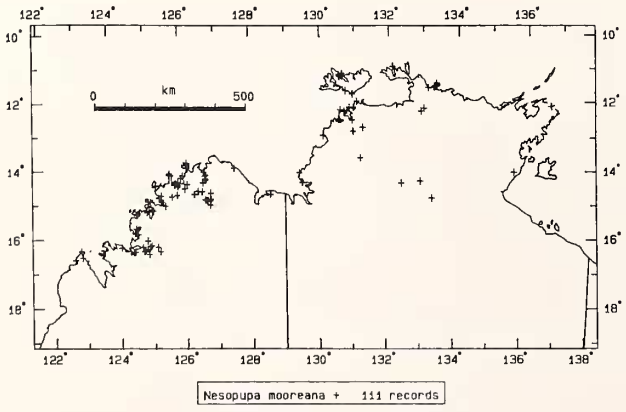

Figure 2

Records of *Nesopupa mooreana* in the Kimberley and "Top End."

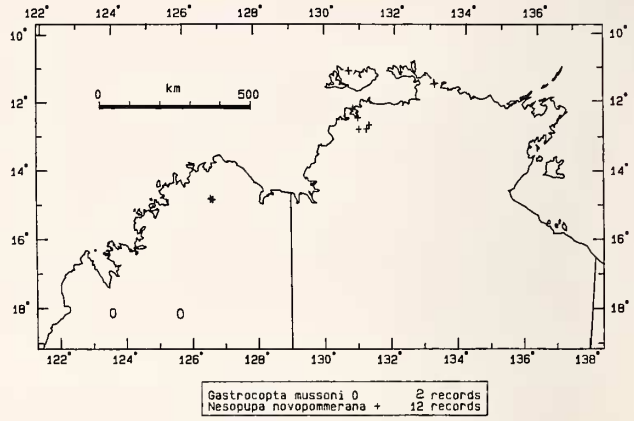

Figure 3

Records of *Nesopupa novopommerana* and *Gastrocopta mussoni* in the Kimberley and "Top End." *Nesopupa novopommerana* has been recorded from New Britain, Bismarck Archipelago, and Tanimbar Island. *Gastrocopta mussoni* has been recorded elsewhere only from Mt. Morgan, Queensland.

extralimital records for both genera and species was equally surprising.

I recognize 34 native (32 named) and two introduced species that belong to eight genera. Some additional taxa were collected in the Cape York Peninsula and along the Gulf of Carpentaria in a 1988 survey. Although brief mention is made of them below, it was not possible to prepare formal descriptions or add their localities to the distribution maps at this time.

A list of the recognized taxa and references to recent literature and illustrations are given in Appendix 1. One additional genus, the Queensland to New South Wales plus New Caledonia *Cylindrovertilla* O. Boettger, 1880,

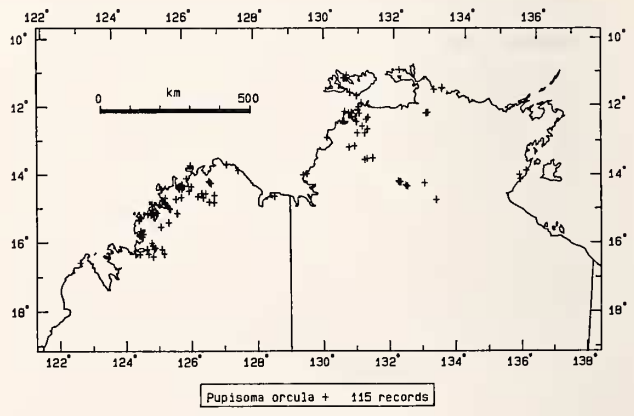

Figure 4

Records of *Pupisoma orcula* in the Kimberley and "Top End." Extralimital range is from India and Japan to New Guinea, Hawaii, and Tuamotu Islands.

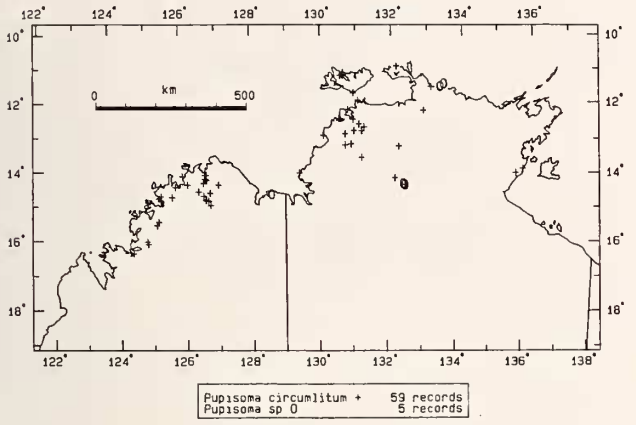

Figure 5

Records of *Pupisoma circumlitum* and *Pupisoma* sp. in the Kimberley and "Top End." *Pupisoma circumlitum* is found also from the Gulf of Carpentaria and Torres Strait south as far as Grafton, New South Wales. *Pupisoma* sp. has not been recorded elsewhere.

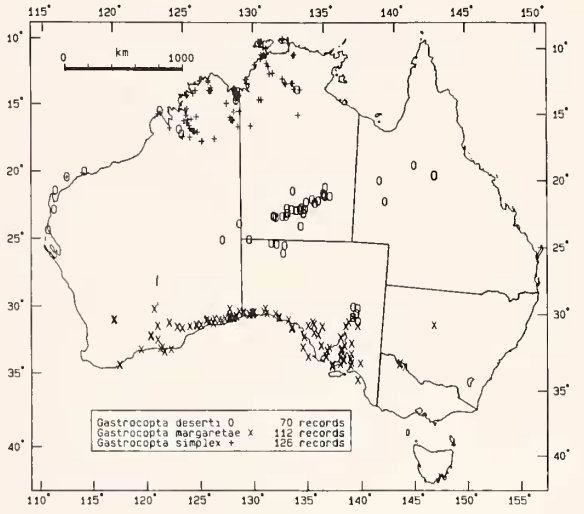

Figure 7

All confirmed records of *Gastrocopta deserti, G. margaretae,* and *G. simplex.*

could not be reviewed because of limited material in collections; and two unquestionably valid New South Wales species, *Gastrocopta strangeana* Iredale, 1937 (= *strangei* Pfeiffer, 1854, *non* Benson, 1853) and *Gastrocopta hedleyi* Pilsbry, 1917, are omitted for the same reason. References to these, and a few additional names that probably are synonyms, also are listed in Appendix 1.

PREVIOUS STUDIES

The classic world monograph of the pupilloid land snails included systematic reviews of Australian taxa (PILSBRY, 1916–1918; 1920–1921; 1922–1926). Pilsbry provided excellent illustrations, a masterly review of previous literature, and many comments about affinities of the Australian species. Very little anatomical data was available for any pupilloids, and none for members of the Australian fauna.

A biogeographic summary of the pupilloid taxa was presented in PILSBRY (1934–1935:139–169). His opening statement is worth repeating: "The family Pupillidae is

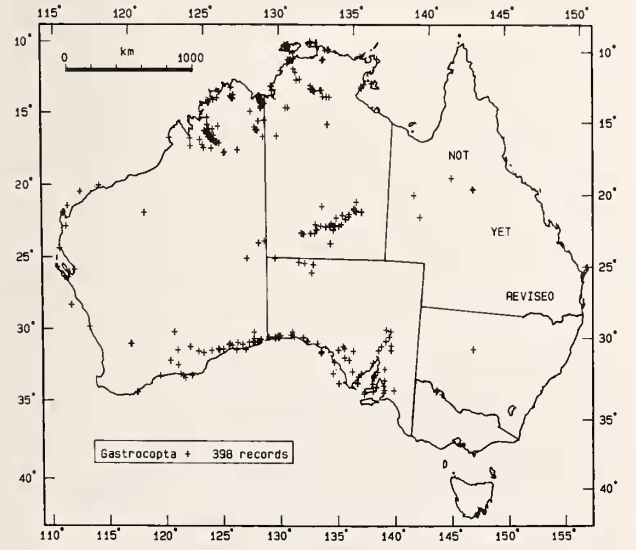

Figure 6

Records of *Gastrocopta* in Australia (revised species only).

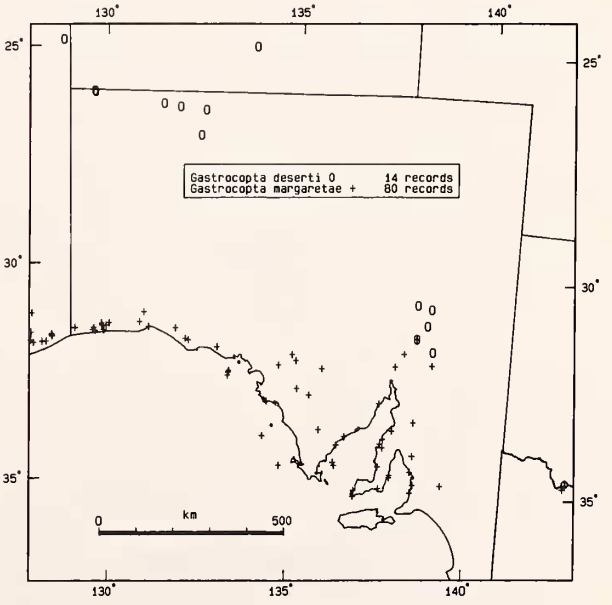

Figure 8

Records of *Gastrocopta deserti* and *G. margaretae* in South Australia and bordering areas.

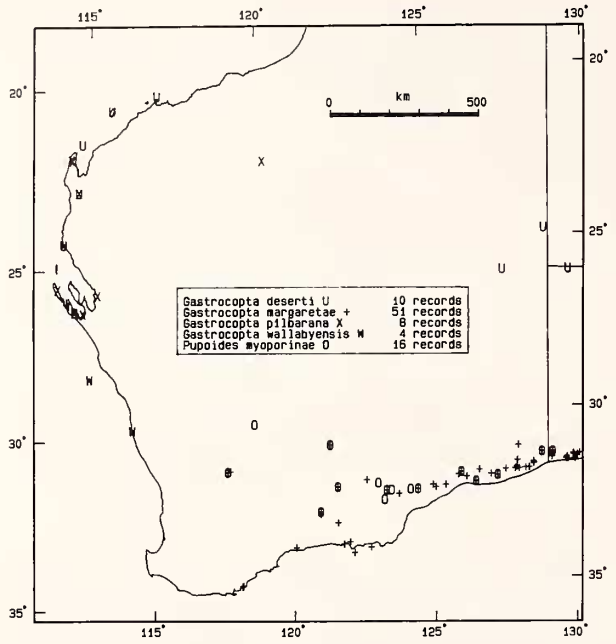

Figure 9

Records of *Gastrocopta deserti, G. margaretae, G. pilbarana, G. wallabyensis,* and *Pupoides myoporinae* in Western Australia below 80 Mile Beach.

essentially a group of the northern continents. The data now at hand indicate Eurasia as the main area of evolution and radiation. All of the major groups (subfamilies) occur in this continent. Of about 50 genera recognized in the family, 38, or about 75 percent, are represented in Eurasia, either living or as Tertiary fossils."

"The southern continents and islands have, in addition to northern genera which extend into them, only about 8

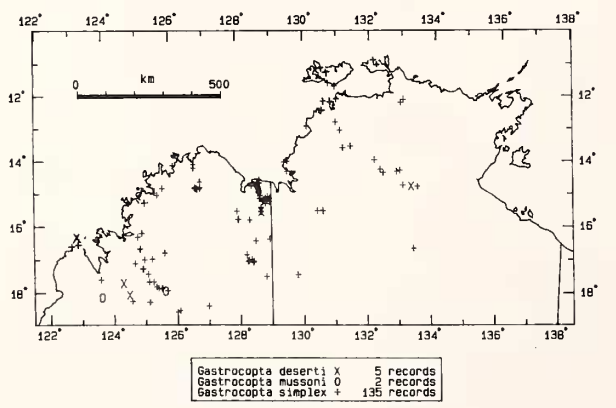

Figure 10

Records of *Gastrocopta deserti, G. mussoni,* and *G. simplex* in the Kimberley and "Top End."

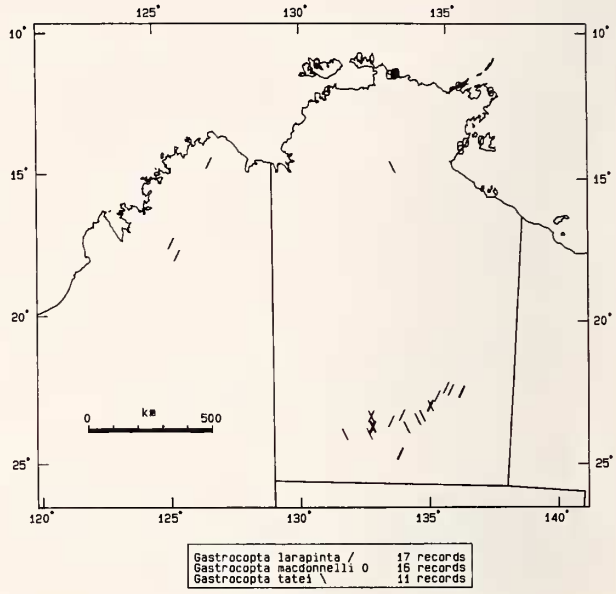

Figure 11

Records of *Gastrocopta larapinta, G. macdonnelli,* and *G. tatei* in the Kimberley and Northern Territory. *Gastrocopta macdonnelli* also occurs from Torres Strait to Townsville, Queensland.

endemic genera. . . . There is no trace of Antarctic elements suggesting dispersal via Antarctica" (PILSBRY, 1934–1935: 139–140).

In a series of nomenclatural notes, checklists, and faunal surveys, IREDALE (1930, 1933, 1937a, b, 1939, 1940, 1941)

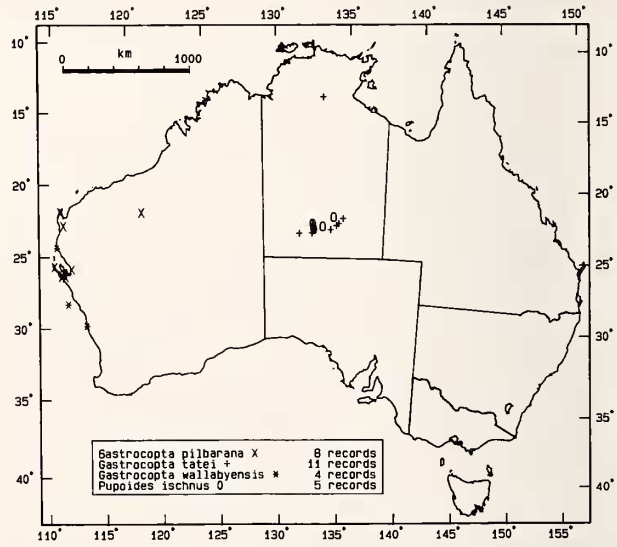

Figure 12

Records of rare Australian species: *Gastrocopta pilbarana, G. tatei, G. wallabyensis,* and *Pupoides ischnus.*

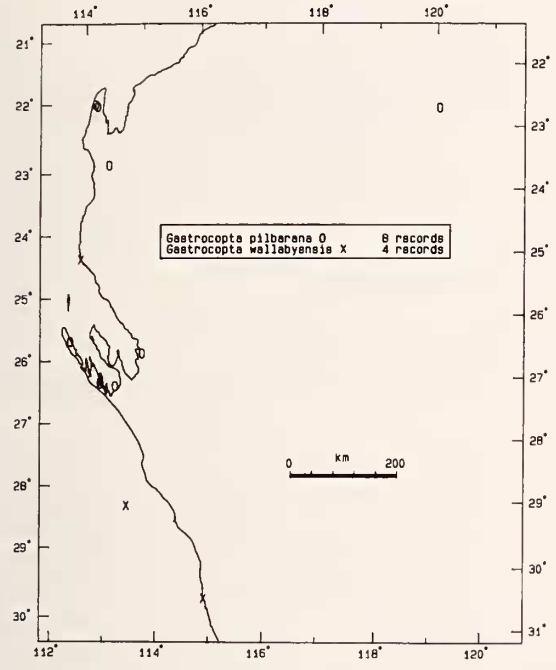

Figure 13

Records of *Gastrocopta pilbarana* and *G. wallabyensis* along the coast of central Western Australia.

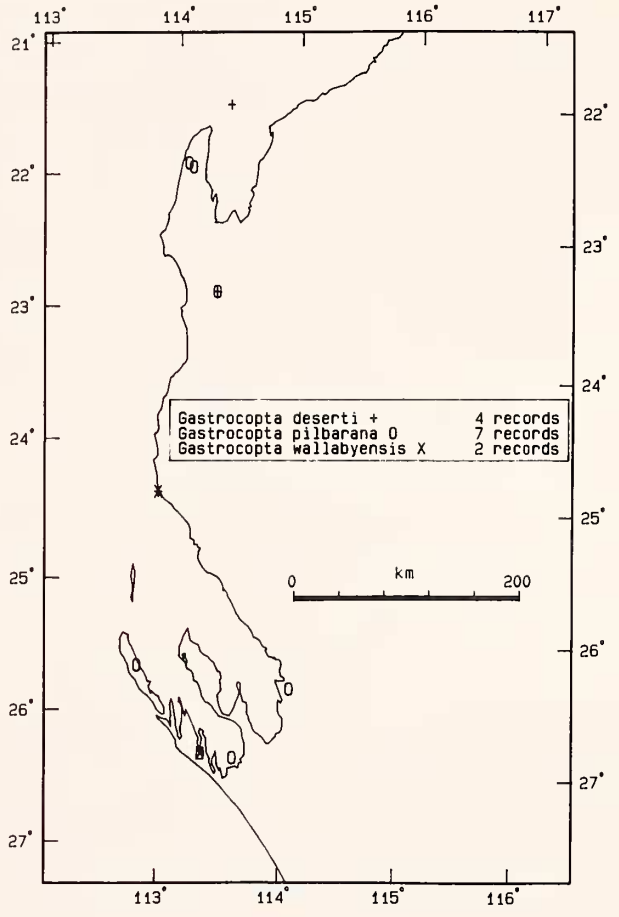

Figure 14

Records of *Gastrocopta deserti, G. pilbarana,* and *G. wallabyensis* in Western Australia between Shark Bay and the North West Cape.

proposed eight new generic units (*Famarinia, Gyrodaria, Imputegula, Omegapilla, Papualbinula, Somniopupa, Themapupa,* and *Wallivertilla*); 12 new species or subspecies; and one replacement name (*Gastrocopta strangeana*). The net effect of the generic names was to "isolate" the Australian taxa from those living elsewhere. None of Iredale's new genera are considered valid, and 11 of his 12 new taxa are placed in synonymy. The 12th, *Cylindrovertilla fabreana boynensis* Iredale, 1937, may prove to be valid. His replacement name is accepted.

In the period since Iredale's taxonomic splitting, the Australian pupilloids have had brief biogeographic mention in McMichael & Iredale (1969) and Bishop (1981: 934–936, 940); cursory comments in the faunistic handbooks of Smith & Kershaw (1979:102–110; 1981:65, 1926); a brief historical review of knowledge concerning the South Australian land mollusks (Smith, 1985); and the three revisions by Solem (1981, 1986, 1989).

No anatomical data have been recorded, leaving questions of both family and generic level classification and phylogeny completely unanswerable at this time. The degree of classificatory uncertainty is demonstrated by Table 1, which lists the family level units of pupilloids used for Australian taxa in the last half century. Table 2 allocates the Australian genera to the subfamilies used in the conservative classification of Pilsbry (1948), which I have chosen to follow in this study. It is not possible to suggest ancestor-descendant relationships among these genera or to construct meaningful phylogenies. The few published anatomical studies on Holarctic taxa do show that considerable structural variation exists, but too few taxa have been studied to permit phylogenetic studies of the main Holarctic groups, much less the world fauna.

MATERIALS

All records utilized in this study are based upon specimens examined by the author. The early literature contains many misidentifications, and thus only specimen-confirmed localities have been included. The records listed by Solem (1981, 1986, 1989) have been supplemented by a review of the collections in the Western Australian Museum, Perth; South Australian Museum, Adelaide; Australian Museum, Sydney; Museum of Victoria, Melbourne; Queensland Museum, Brisbane; and the private collections of Fred Aslin (Mount Gambier, South Australia) and Vince Kessner (Adelaide River, Northern Territory). Extensive collections in 1988 from continental shelf islands along the

Table 1

Previous family level classifications of pupilloid taxa.

Iredale (1940)	Pilsbry (1948)	Zilch (1959)	Solem (1978)	Tillier (1989)
		Pupillacea	Pupillacea	Pupillacea
Gastrocoptidae	Pupillidae	Vertiginidae	Pupillidae	Pupillidae
Cylindrovertillidae	Nesopupinae	Nesopupinae		Chondrinoidea
Pupoididae	Gastrocoptinae	Gastrocoptinae		Chondrinidae
Pupisomidae	Pupillinae	Hypselostominae		Vertiginidae
		Pupillidae		
		Pupillinae		
		Valloniidae		
		Acanthinulinae		

Kimberley coast by Vince Kessner and Alan Longbottom; in the Napier and Oscar Ranges in the south Kimberley by R. A. D. Cameron; and the Gulf of Carpentaria and Cape York Peninsula by L. Price, V. Kessner, and J. Stanisic are referred to in the text, but were received for study too late to be added to the maps.

METHODS

All distributional records with good locality data were entered into the FLORAPLOT program at the Western Australian Wildlife Research Centre, Wanneroo, Western Australia. (A hard copy printout of all entered records is located in the Division of Invertebrates, Field Museum of Natural History, Chicago, Illinois.) They were entered to the nearest minute of longitude and latitude if a town, mountain, or homestead was involved or to the nearest second of longitude and latitude if the locality data were more precise, *i.e.,* a spring, creek bend, isolated hill, dam, or well. Localities such as Roebuck Bay, the type locality of *Nesopupa mooreana* (E. A. Smith, 1894), and "Murray River," could not be localized within a minute of latitude and longitude, and thus are not included in the data base.

Table 2

Classification used for Australian pupilloid genera.

Family Pupillidae
Subfamily Nesopupinae
Nesopupa
Pupisoma
Cylindrovertilla
Subfamily Gastrocoptinae
Gastrocopta
Pumilicopta
Gyliotrachela
Subfamily Pupillinae
Pupilla
Pupoides
Glyptopupoides

Maps were printed using a Hewlett-Packard digital plotter. (All printed maps are now located in the Division of Invertebrates, Field Museum of Natural History.) Many maps were designed to indicate broad scale distributions (Figures 2–7, for example), others to show details of diversity and species sympatry (Figures 9, 11, 13, 14, 27, 28, 31). Judicious selection of compatible symbols for different species, such as "+" and "0" or "/" and "\", means that microsympatry to within a second of latitude and longitude appears on the maps as an "⊕" or an "×". Species with complex diversity associations or very wide distributions may thus appear on several maps. Other species may be used as convenient "markers" on several maps against which to compare distributions of widely dispersed species whose many overlapping records would make joint display on one map extremely confusing or incomprehensible.

DISTRIBUTION PATTERNS

Some area terms will not be familiar to non-Australian readers. The following definitions should suffice (see Figure 1):

Dampierland—Peninsula in Western Australian from Broome to Cape Leveque, ca. 16° to 18°S, 122° to 123°30′E.

Kimberley—The northern portion of Western Australia, 13°30′ to 19°S, 123°30′ to 120°E.

"Red Centre"—Mountainous parts of Western Australia, South Australia, and Northern Territory, 20° to 26°S, 128° to 137°E.

"Top End"—Tropical area of the Northern Territory above the Roper River, ca. 10° to 16°S, 129° to 137°E.

It is easy to forget that Australia is essentially identical in size to the mainland United States (exclusive of Alaska). Despite the number of records, faunal surveys are still very incomplete. Thus, initial commentary must be made as to the adequacy of distributional data and whether blank spots on a map indicate species absence, collecting absence, or revisionary work absence.

Plotted distributions of two genera, *Gastrocopta* Wol-

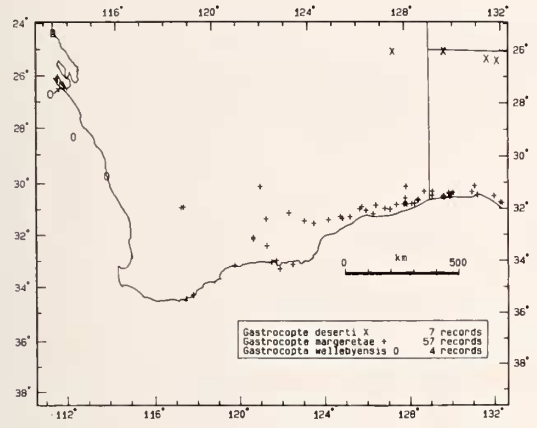

Figure 15

Records of *Gastrocopta deserti, G. margaretae,* and *G. wallabyensis* in southern Western Australia.

laston, 1878 (Figure 6) and *Pupoides* Pfeiffer, 1854 (Figure 24), illustrate the above points. *Pupoides* has been recorded from many localities in coastal Queensland and eastern New South Wales, whereas *Gastrocopta* appears to be absent from these areas. In fact, the material of *Gastrocopta* from these regions is somewhat limited [except for the introduced *G. pediculus* (Shuttleworth, 1852)], but the species have not been revised. Neither genus is present in Tasmania or nearly all of Victoria, nor in the humid southwest corner of Western Australia (except for a few islands). Collecting in these regions has been extensive, so that "genus absence" can be accepted. Neither genus shows extensive records along the west side of the Cape York Peninsula and Gulf of Carpentaria. Collections from these areas made late in 1988 contain both genera, indicating that this was a collecting gap.

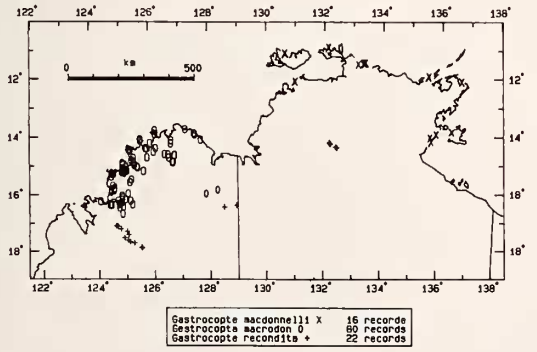

Figure 16

Records of *Gastrocopta macdonnelli, G. macrodon,* and *G. recondita* in the Kimberley and "Top End." *Gastrocopta macdonnelli* also ranges from Torres Strait to Townsville, Queensland; *G. macrodon* has been found at Milne Bay, Papua, and in the Louisiade Archipelago; and *G. recondita* is recorded from the Aru and Tanimbar Islands, plus Haruku near Ambon, Indonesia.

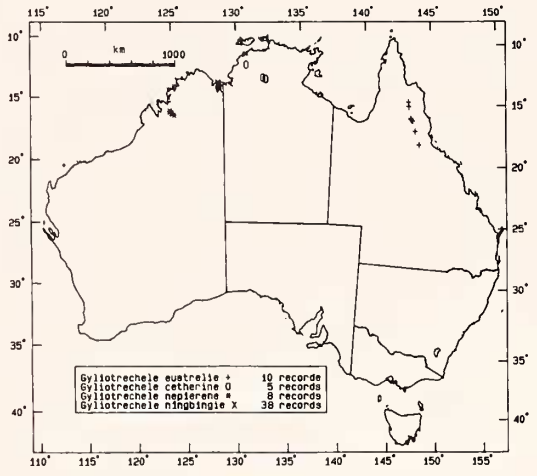

Figure 17

Ranges of *Gyliotrachela australis, G. catherina, G. napierana,* and *G. ningbingia* in Australia.

The interior basins of Western Australia, southwest interior Queensland, and far north of South Australia below the Everard to Tomkinson Ranges are malacologically unexplored and quite probably nearly "snail-free" territory. At most one can expect to find scattered relict colonies. In contrast, the many Flinders Ranges and Eyre Highway associated records reflect both local abundance and many visits by collectors.

The above caveats should be kept in mind during all of the following discussions.

Generic and Species Ranges

A brief discussion of extralimital distributions precedes the description of Australian ranges. The generic sequence follows that of Table 2.

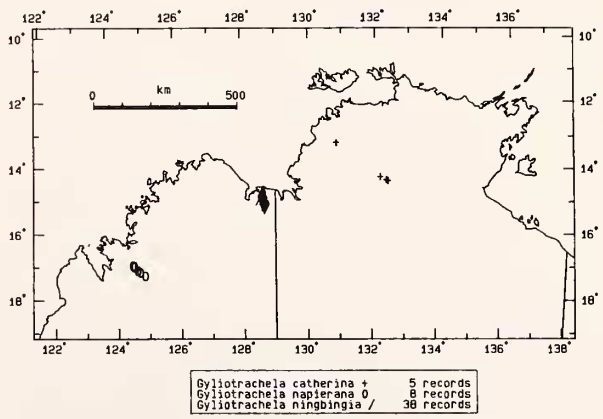

Figure 18

Records of *Gyliotrachela catherina, G. napierana,* and *G. ningbingia* in the Kimberley and "Top End."

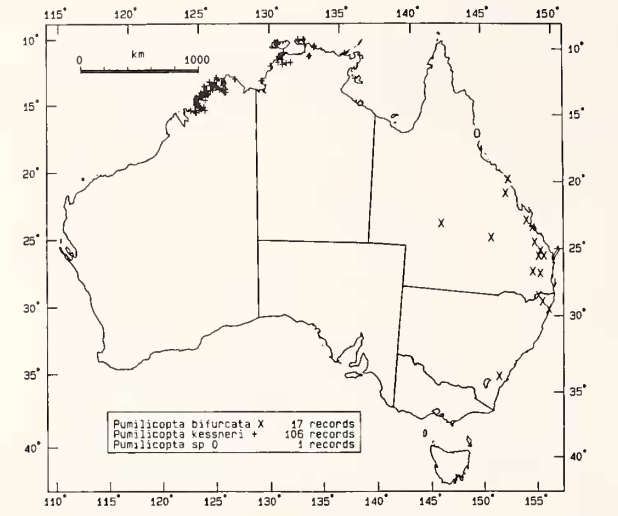

Figure 19

Ranges of *Pumilicopta bifurcata, P. kessneri,* and *Pumilicopta* sp. in Australia.

Nesopupa Pilsbry, 1900, according to the latest world monograph (PILSBRY, 1918–1920:270), has "Distribution: islands of the Pacific, Oriental, and Ethiopian regions, St. Helena. . . . Inhabiting widely separated island groups, there have been several nearly independent centers of evolution, making the construction of a phylogenetic classification exceptionally difficult." There are two, possibly three, species in northern Australia. *Nesopupa mooreana* (Figure 2) is very common in the wetter areas of the Kimberley, reaching south to the tip of Dampierland, and was described from Roebuck Bay, near Broome. It is much less common in the "Top End" of the Northern Territory. *Nesopupa novopommerana* I. Rensch, 1932 (Figure 3) has been collected near Darwin at a few stations in the Drysdale River National Park in the Kimberley. Extralimitally, it lives in the Tanimbar Islands and Bismarck Archipelago. An as yet unidentified *Nesopupa* has been found

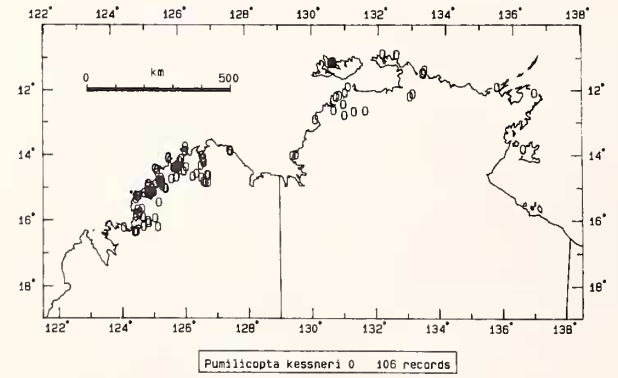

Figure 20

Records of *Pumilicopta kessneri* in the Kimberley and "Top End."

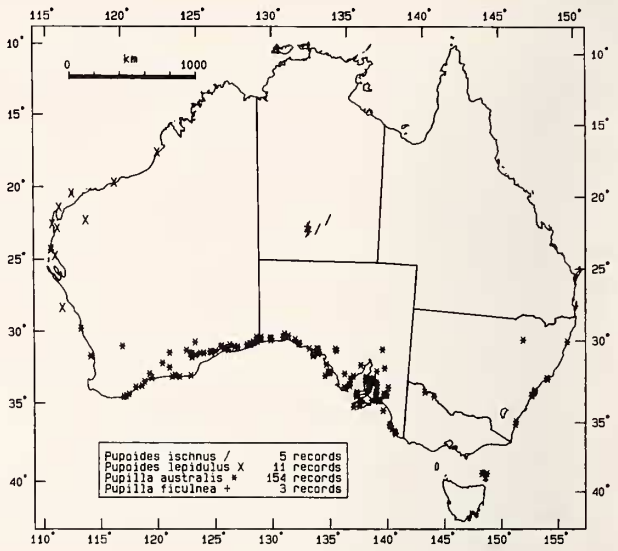

Figure 21

Ranges of *Pupilla australis, Pupilla ficulnea, Pupoides ischnus,* and *Pupoides lepidulus* in Australia.

in Gulf of Carpentaria and Cape York Peninsula collections, establishing a transnorthern Australia distribution for the genus *Nesopupa.*

Pupisoma Stoliczka, 1873, has about 18 species "in tropical and subtropical regions of both hemispheres except in arid districts and oceanic islands" (PILSBRY, 1920–1921: 19). Both *P. orcula* (Benson, 1850) (Figure 4) and *P. circumlitum* Hedley, 1897 (Figure 5) are common in wet areas from Dampierland across the top of Australia to

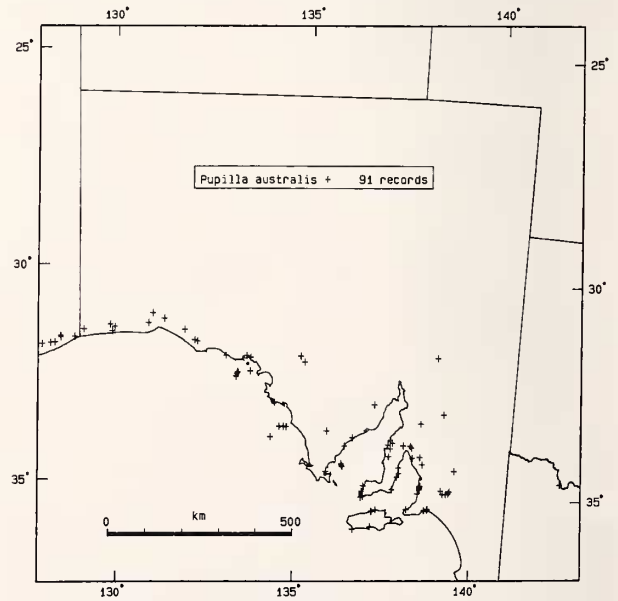

Figure 22

Records of *Pupilla australis* in South Australia.

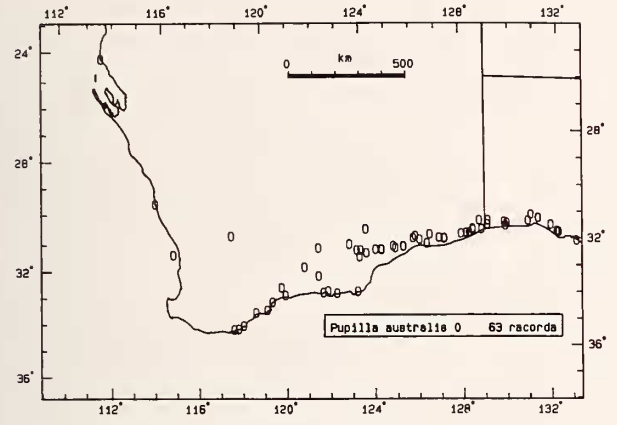

Figure 23

Records of *Pupilla australis* in southern Western Australia.

Torres Strait and northern Queensland, with the former much more abundant. They are conspicuously absent from the drier plains areas. An undescribed species, *Pupisoma* sp. (Figure 5), has been found near Katherine and on Goulburn Island in the Northern Territory, plus the Ningbing Ranges, east Kimberley. Controversy still exists as to whether the New World *P. dioscoricola* (C. B. Adams, 1845) and the Old World *P. orcula* are identical or not. A high degree of accidental transport by man has been hypothesized for *Pupisoma,* but the many rain-forest records in northern Australia strongly suggest natural occurrences. *Pupisoma* is a second transnorthern Australia genus.

Cylindrovertilla O. Boettger, 1880, has not been revised since PILSBRY (1920–1921:43–49). Less than five species have been recorded from New Caledonia, south Queensland, and New South Wales. The limits of distribution and the actual number of species are equally uncertain.

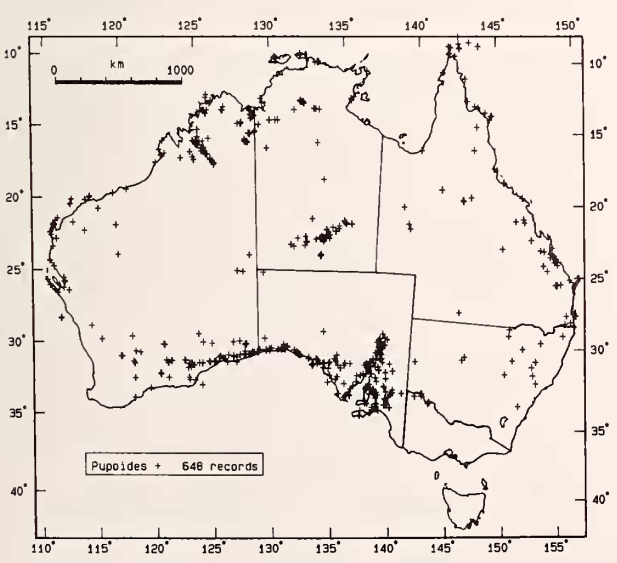

Figure 24

Records of *Pupoides* in Australia.

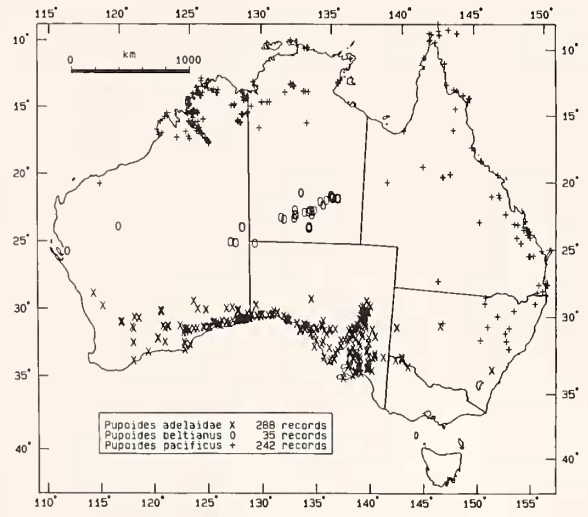

Figure 25

Records of *Pupoides adelaidae, P. beltianus,* and *P. pacificus* in Australia.

Gastrocopta probably has the widest natural range of any land snail genus, being "nearly world-wide in tropical and temperate regions, but wanting on many oceanic islands and in the recent European fauna, though represented there as Oligocene to Pliocene fossils" (PILSBRY, 1948:871). A few species have been widely disseminated by man, and two of these have reached Australia. *Gastrocopta servilis* (Gould, 1843), originally from the West Indies, has been collected near Broome and in Queensland;

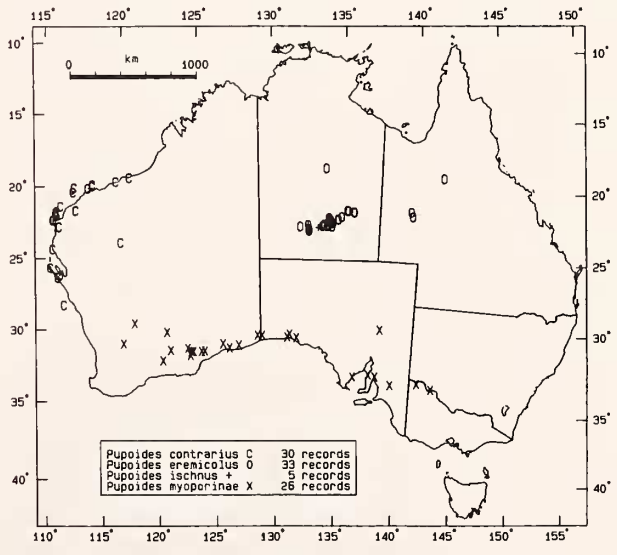

Figure 26

Records of *Pupoides contrarius, P. eremicolus, P. ischnus,* and *P. myoporinae* in Australia.

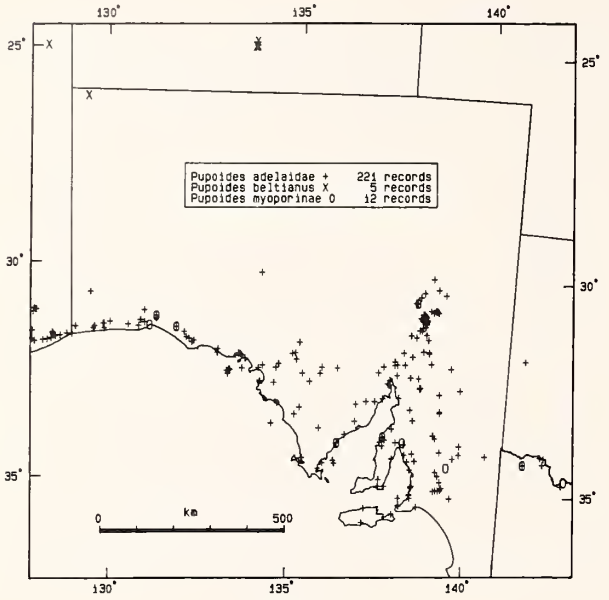

Figure 27

Records of *Pupoides adelaidae, P. beltianus,* and *P. myoporinae* in South Australia.

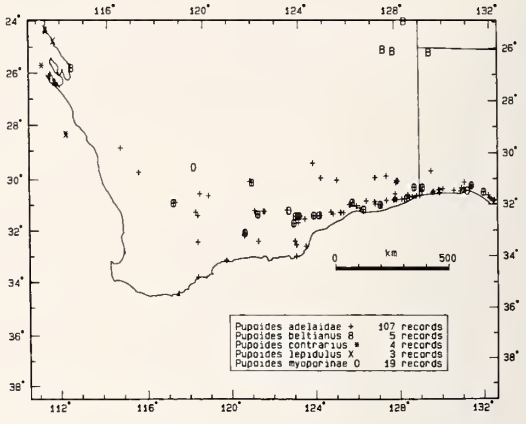

Figure 28

Records of *Pupoides adelaidae, P. beltianus, P. contrarius, P. lepidulus,* and *P. myoporinae* in southern Western Australia.

although listed under a variety of names, it is a common introduced species of New Guinea, Indonesia, and on many Pacific Islands (SOLEM, 1989:483–484). *Gastrocopta pediculus* is the most common Pacific Island species and has been present in Queensland and New South Wales for more than a century, again recorded previously under various names (SOLEM, 1989:486–487).

Gastrocopta is the most speciose of the Australian pupilloid genera, with 11 recognized species, plus two eastern states species, *G. strangeana* and *G. hedleyi,* that have not been revised. Extensive collections from the Gulf of Carpentaria and Cape York Peninsula remain to be studied. Probably additional species will be recognized.

Except for the humid southern areas (Figure 6), *Gastrocopta* is found throughout Australia. *Gastrocopta margaretae* (Cox, 1868) (Figure 7) is basically south coast; *G. deserti* (Figure 7) is "Red Centre" and western Queensland, but meets *G. margaretae* in the Flinders Ranges of South Australia (Figure 8), *G. pilbarana* Solem, 1986 on the west coast (Figure 9), and *G. simplex* Solem, 1989 (Figure 10) in the Kimberley. There are no other southern species. The "Red Centre" has *G. larapinta* (Tate, 1896) and *G. tatei* Pilsbry, 1917 (Figure 11), both of which have a few "dry fringe" records in the Kimberley and "Top End." The west coast has two species of relatively limited ranges, *G. pilbarana* and *G. wallabyensis* (E. A. Smith, 1894) (Figures 9, 12–15). Finally, there are a number of Kimberley-"Top End" species. *Gastrocopta simplex* (Figures 7, 10) is widely distributed; *G. mussoni* Pilsbry, 1917 (Figures 10, 32) lives on the desert fringes of the southwest Kimberley and also has been recorded from Mt. Morgan, Queensland; *G. macdonnelli* (Brazier, 1875) (Figure 16) lives in coastal areas of the "Top End" and then ranges east to Torres Strait and northern Queensland; *G. macrodon* Pilsbry, 1917 (Figure 16) is restricted to wetter areas of the Kimberley, then recurs in the Louisiade Archipelago and Milne Bay, Papua; and *G. recondita* (Tapparone-Canefri, 1883) (Figure 16) lives in dryer portions of the south Kimberley and "Top End," with an extralimital extension to the Aru and Tanimbar Islands, plus Haruku near Ambon in the Moluccas. The range of *Gastrocopta* thus covers most of Australia.

Gyliotrachela ranges from Burma and Malaya through Indonesia to Timorlaut and the Tanimbar Islands, with a small radiation of four widely separated species in northern Australia (Figures 17, 18). All species are strictly limestone associated. The "Top End"-Kimberley taxa are from drier fringes. *Gyliotrachela* thus has an interrupted north Australian distribution, mainly from inland dry areas.

Pumilicopta Solem, 1989, has species on Sumba and Timor, plus *P. kessneri* Solem, 1989, in wet areas of the Kimberley and "Top End," an undescribed species from the Bellenden Ker Ranges, and *P. bifurcata* Solem, 1989, from scattered areas in Queensland and New South Wales (Figures 19, 20). Additional taxa have been collected recently in Cape York and Gulf of Carpentaria regions, thus giving *Pumilicopta* a transnorthern Australian and eastern states range.

Pupilla Leach, 1828, known from various parts of "North America, Eurasia, Africa, Australia, almost wholly in temperate and cold regions . . . is a widely distributed group, nowhere numerous in species, but generally abundant in individuals" (PILSBRY, 1948:927). The two Australian species have very different ranges. *Pupilla australis* (Adams & Angas, 1864) (Figures 21–23) has a south coast range with isolated records as far north as Carnarvon on the west coast; in the eastern states it reaches northern New South Wales and has been found on some islands in Bass Strait, Tasmania. *Pupilla ficulnea* (Tate, 1894) is a rare

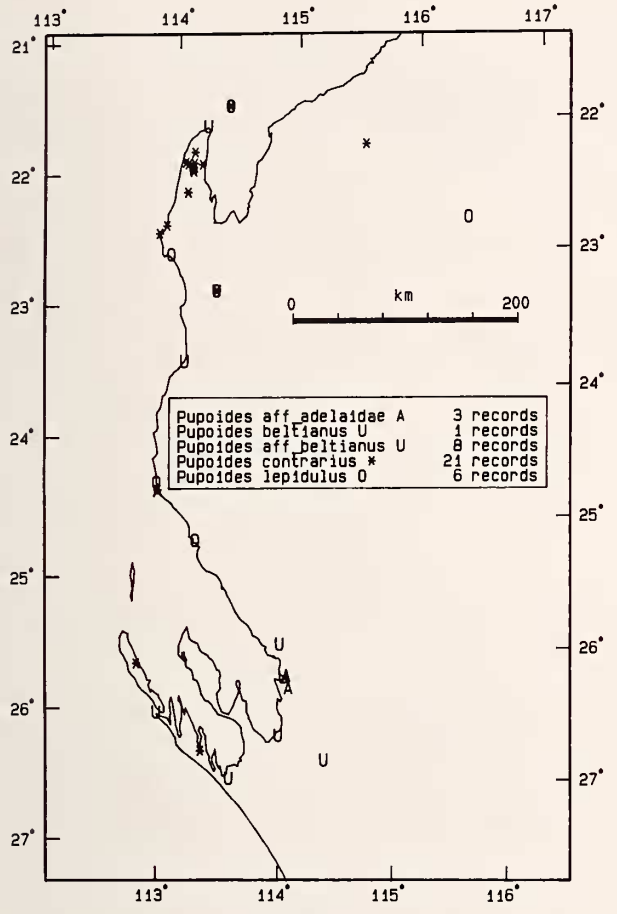

Figure 29

Records of *Pupoides* species and forms in the Shark Bay to North West Cape area of Western Australia.

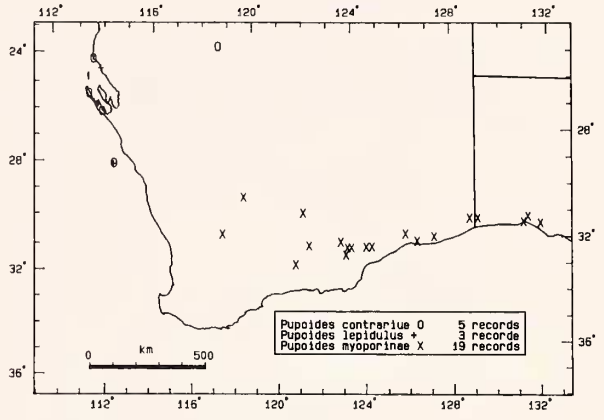

Figure 30

Records of *Pupoides contrarius, P. lepidulus,* and *P. myoporinae* in southern Western Australia.

species of limited range in the "Red Centre" (Figure 21). *Pupilla* thus has a southern range with an isolated species in the seasonally cold "Red Centre."

Pupoides ranges within Australia as widely as *Gastrocopta* (compare Figures 6 and 24) and is the second most speciose genus of Australian pupilloids, with eight recognized species. Found on "all of the continents except Europe" (PILSBRY, 1948:920), "*Pupoides* is mainly a tropical and subtropical genus of arid regions or of relatively dry stations in humid areas. . . . The distribution of *Pupoides* is remarkably discontinuous . . . [and] the absence of the genus in southeastern Asia and East Indies [= Indonesia] leaves the Australian herd profoundly isolated" (PILSBRY, 1920–1921:109). *Pupoides pacificus* (Pfeiffer, 1846) (Figure 25) has a continuous range of Dampierland to Torres Strait and well into New South Wales (many additional Cape York and Gulf of Carpentaria collections were made in 1988). *Pupoides beltianus* (Tate, 1894) (Figure 25) has a "Red Centre" to Shark Bay range. *Pupoides adelaidae* (Adams & Angas, 1864) (Figure 25) is very common between Morawa (northeast of Perth, Western Australia) to the Murray River, Victoria. *Pupoides eremicolus* (Tate, 1894) (Figure 26) is a "Red Centre" and western Queensland species. *Pupoides myoporinae* (Tate, 1880) (Figure 26) is a second south coast species, but less common than *P. adelaidae* and with a shorter range. *Pupoides lepidulus* (Adams & Angas, 1864) (Figure 21) and *P. contrarius* (E. A. Smith, 1894) (Figure 26) both have central west coast ranges in Western Australia. Finally, *P. ischnus* (Tate, 1894) (Figures 21, 26) is a rare species of the "Red Centre."

A notable aspect of distribution in *Pupoides* is that wherever species ranges overlap, a dextrally coiled and a sinistrally coiled species are involved. The sympatric pairs are:

Area	Dextral species	Sinistral species
South coast	*adelaidae*	*Myoporinae*
West coast	*lepidulus*	*contrarius*
"Red Centre"	*beltianus*	*eremicolus* & *ischnus*

The only exception concerns *P. pacificus,* a dextral species, and the only *Pupoides* found in northern Australia and the eastern states. One sinistral population of a *Pupoides* was collected on Cassini Island, Admiralty Gulf, Kimberley in the 1890s (PILSBRY, 1920–1921:144), and it was collected again in 1988. Referred to as "form *sinistralis*" by Pilsbry, its taxonomic status remains to be determined.

Glyptopupoides is the only Australian restricted endemic genus. Originally considered to be a land prosobranch, the same species was redescribed by PILSBRY (1922–1926:252–253) and assigned to a new subgenus of *Pupoides,* which IREDALE (1937a:304) raised to generic rank in a checklist. *Glyptopupoides egregia* (Hedley & Musson, 1891) has a remarkable disjunct distribution, with one cluster of records from the fringes of inland rain-forest patches in the Kimberley (Figure 31), and an extended east coast range (Figure 32). Collecting in the Cape York area has marginally extended its range northwards. The disjunct Kimberley and Queensland-New South Wales range of *Glyp-*

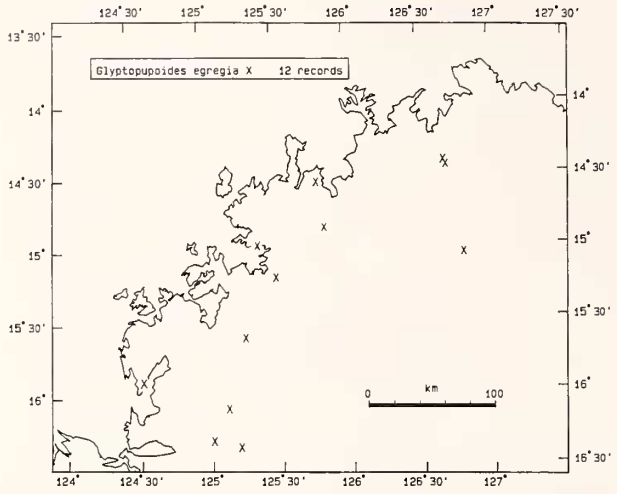

Figure 31

Records of *Glyptopupoides egregia* in the Kimberley and "Top End."

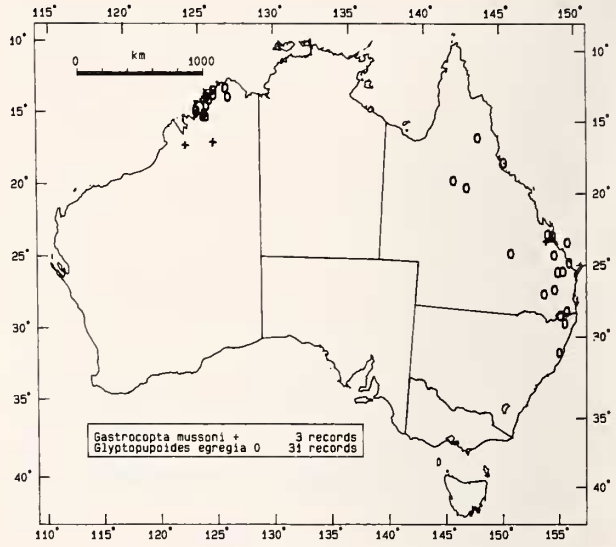

Figure 32

Ranges of *Gastrocopta mussoni* and *Glyptopupoides egregia* in Australia.

topupoides is nearly matched by that of *Gastrocopta mussoni* (Figure 32).

The nine genera thus have a few simple patterns of distribution:

(1) Only *Glyptopupoides* is a restricted endemic in Australia, showing a strikingly disjunct Kimberley and Queensland-New South Wales range (Figure 32);

(2) Two genera have regional extralimital ranges: *Cylindrovertilla* is found in New Caledonia and then the Queensland-New South Wales arc; and *Pumilicopta* has a Sumba and Timor range in Indonesia, followed by a continuous wetter forest range from the Kimberley to Torres Strait and into southern New South Wales (Figure 19);

(3) *Gyliotrachela* is characteristic of at least seasonally wet limestone areas from Burma through Indonesia, and has four isolated endemic species scattered across northern Australia (Figure 17);

(4) *Pupisoma* has a pantropical and pansubtropical distribution, some of which may be caused by accidental introduction on plants carried about by man—in Australia it has a wet forest transnorthern Australia range (Figures 4, 5);

(5) *Nesopupa* ranges from Africa and India to the furthest Pacific Islands, with limited wet forest northern Australian distribution (Figures 2, 3);

(6) *Pupilla* has a disjunct multicontinent distribution, with localized abundance, but not diversity, in temperate and colder regions, which fits its south coast and restricted "Red Centre" range in Australia (Figure 21); and

(7) Both *Gastrocopta* (Figure 6) and *Pupoides* (Figure 24) are nearly world-wide, but each has a few odd distributional gaps. Both genera are found throughout the pupilloid inhabitable parts of Australia, but not in Tasmania, most of Victoria, or the humid southwest corner of Western Australia.

Regional Summary

On a regional basis, tropical northern Australia from the tip of Dampierland to Torres Strait and then south along the coastal forests of Queensland has the most diverse fauna, with: (1) *Pupisoma, Nesopupa, Pumilicopta, Gastrocopta,* and *Pupoides* ranging, at least in wetter areas, across the continent; (2) *Gyliotrachela* having a scattering of isolated species in seasonally dry limestone areas; and (3) *Glyptopupoides* showing a disjunct Kimberley, then Queensland-New South Wales range. Only the eastern *Cylindrovertilla* and the cool-temperate genus *Pupilla* are absent.

The at least seasonally wet eastern forests of Queensland and New South Wales, between the Great Dividing Range and the Pacific Ocean, have *Pupisoma, Nesopupa,* and one limited range species of *Glyliotrahela* in the north; *Glyptopupoides, Pupoides, Cylindrovertilla, Pumilicopta,* and a few *Gastrocopta* extending well to the south; and limited records of *Pupilla* extending north along mainly coastal New South Wales from its trans-Australian south coast range. Any given area may have fewer genera present than do the northern fringe sections, but the eastern wet forests include the whole range of pupilloid genera.

The south coast, from the New South Wales-South Australia border to Albany, Western Australia, has only three genera, *Gastrocopta, Pupoides,* and *Pupilla.* The "Red Centre" and the west coast of Western Australia from just south of Geraldton to Broome and Dampierland have the same limited group of genera present. Thus, the southern half of Australia, except for a limited extension south in the humid forests of New South Wales, has only three of the nine pupilloid genera.

Patterns of species diversity are similar. Four northern

Table 3

Species distribution patterns.

NORTHERN AUSTRALIA
- Wet and intermediate areas (moving west to east)
  - Trans-Australia
    - *Pupisoma orcula*
    - *Pupisoma circumlitum*
    - *Pupoides pacificus*
  - Kimberley only
    - *Gastrocopta macrodon*
    - *Glyptopupoides egregia* (also QLD and NSW)
  - Kimberley and "Top End"
    - *Nesopupa mooreana*
    - *Nesopupa novopommerana*
    - *Pumilicopta kessneri*
    - *Pupisoma* sp.
  - "Top End" and Queensland
    - *Gastrocopta macdonnelli*
  - Queensland
    - *Pumilicopta* sp.
    - *Gyliotrachela australis*
    - *Pupisoma orcula* (from trans-Australia)
    - *Pupisoma circumlitum* (from trans-Australia)
    - *Gastrocopta mussoni* (from dry Kimberley)
    - unrevised *Gastrocopta* and *Pumilicopta*
  - Queensland-New South Wales
    - *Pumilicopta bifurcata*
    - *Gastrocopta strangeana*
    - *Gastrocopta hedleyi*
    - *Cylindrovertilla* spp.
    - *Pupoides pacificus* (from trans-Australia)
    - *Glyptopupoides egregia* (also Kimberley)
- Dry fringes (moving west to east)
  - Kimberley
    - *Gastrocopta mussoni* (also S QLD)
    - *Gastrocopta larapinta* (from "Red Centre")
    - *Gastrocopta deserti* (from "Red Centre")
    - *Gyliotrachela napierana*
    - *Gyliotrachela ningbingia*
  - Kimberley and "Top End"
    - *Gastrocopta simplex*
    - *Gastrocopta recondita*
    - *Gastrocopta deserti* (from "Red Centre")
  - "Top End" only
    - *Gastrocopta tatei* (from "Red Centre")
    - *Gyliotrachela catherina*
  - Queensland
    - *Gastrocopta deserti* (from "Red Centre")
  - Kimberley and Queensland disjunct
    - *Gastrocopta mussoni*
    - *Glyptopupoides egregia*

"RED CENTRE"
- *Gastrocopta deserti*
- *Gastrocopta tatei*
- *Gastrocopta larapinta*

Table 3

Continued.

- *Pupoides beltianus*
- *Pupoides eremicolus*
- *Pupoides ischnus* (limited range)
- *Pupilla ficulnea* (limited range)

WEST COAST AND PILBARA
- *Gastrocopta deserti* (from "Red Centre")
- *Gastrocopta pilbarana*
- *Gastrocopta wallabyensis*
- *Pupoides contrarius*
- *Pupoides lepidulus*

SOUTH COAST AND FLINDERS
- *Gastrocopta deserti* (from "Red Centre")
- *Gastrocopta margaretae*
- *Pupilla australis*
- *Pupoides adelaidae*
- *Pupoides myoporinae*

Australian species have extralimital ranges. *Pupisoma orcula* extends at least to southeast Asia and may be circumtropical; *Nesopupa novopommerana* has been collected on the Tanimbar Islands and New Britain, Bismarck Archipelago; *Gastrocopta macrodon* is restricted to the wet Kimberley, but then appears at Milne Bay, Papua, and in the Louisiade Archipelago; and *G. recondita,* from the dry south fringes of the Kimberley and "Top End," also lives in the Aru and Tanimbar Islands plus on Haruku near Ambon in the Moluccas, Indonesia.

Only two species show notable disjunctions within Australia. *Gastrocopta mussoni* has been recorded from two localities in the desert fringes of the south Kimberley and also from Mt. Morgan, Queensland. *Glyptopupoides egregia* has a fairly wide distribution on the fringes of mainly inland rain-forest patches in the Kimberley and an extensive Queensland-New South Wales range.

The general patterns of species distributions are summarized in Table 3. Nineteen of the 32 named species are present in some part of the Kimberley and "Top End," with a distinct difference between the dry fringes and the northern wetter zones. In contrast, the "Red Centre" has only seven species. The south coast and west coast each have four endemics plus an intrusion of *Gastrocopta deserti* from the "Red Centre." Data are inadequate to characterize the pupilloid fauna from the wet forests of Queensland and New South Wales, although that fauna is generically diverse and with at least a modest species radiation.

LOCAL DIVERSITY PATTERNS

Although recent collections from the Gulf of Carpentaria fringes and Cape York region have filled in a major collecting gap and provided many sympatric records, data from that survey are not available for interpretation at this time. Historic records from the literature cannot be depended upon for an accurate depiction of sympatry, and

Table 4

Pupilloid species in Kimberley wet areas.

Species	Island samples (n = 91)		Coastal samples (n = 35)		Inland samples (n = 31)	
	Number	Percent	Number	Percent	Number	Percent
Gastrocopta macrodon	74	81.3	27	77.1	20	64.5
Gastrocopta simplex	9	9.9	1	2.9	5	16.1
Glyptopupoides egregia	2	2.2	2	5.7	8	25.8
Nesopupa mooreana	48	52.7	28	80.0	20	64.5
Pupisoma circumlitum	9	9.9	3	8.6	10	32.3
Pupisoma orcula	32	35.2	25	71.4	23	74.2
Pupoides pacificus	26	28.6	12	34.3	12	38.7
Pumilicopta kessneri	38	41.8	34	97.1	18	58.1

thus comments on the Queensland-New South Wales patterns must be deferred. Preliminary review of the new collections suggests that local diversity rarely reaches four species and that distribution is patchier than in the Kimberley.

Both the south and west coasts of Australia have a limited fauna (Table 3). Both areas have fringe records of the "Red Centre" species *Gastrocopta deserti* (Figures 8, 9, 14, 15), sometimes involving microsympatry with other *Gastrocopta*. The south coast has four species with rather wide ranges: (1) *Pupilla australis* (Figure 21) is more coastal and extends to the coast of New South Wales; (2) *Gastrocopta margaretae* (Fig. 7) inhabits much of the Flinders Ranges, but does not extend as far east or west as does *Pupilla australis*; (3) *Pupoides adelaidae* (Figure 25) extends further inland and westward; and (4) *Pupoides myoporinae* (Figure 26), which is much less abundant, has a less extensive range, and is absent from much of the Eyre Peninsula. The two species of *Pupoides* show occasional sympatry in South Australia (Figure 27), but *P. adelaidae* is much more abundant and widely distributed. In Western Australia (Figure 28), most records of *P. myoporinae* involve sympatry with *P. adelaidae*. In coastal and Eyre Highway sections, sympatry of all four species is not unusual, with inland records showing loss of the more coastal taxa. *Pupilla australis* (Figures 22, 23) has inland records in South Australia but mainly coastal records in Western Australia.

Interpretation of west coast records is premature, because many collections consist only of sifted drift material, and thus potentially represent mixed habitat information. Records are few in number, reflecting both the harsh habitat and the comparatively limited collecting done in this region. From Shark Bay to just north of the North West Cape, there are four *Pupoides* (Figure 29) recognized (see SOLEM, 1986:107–115): *Pupoides lepidulus* (Figure 21) and *P. contrarius* (Figure 26), both restricted endemics; an apparent intrusion of the "Red Centre" species *P. beltianus* (Figure 25); and a very few records of the south coast *P. adelaidae*. The endemics (Figures 28, 30) often are microsympatric. The otherwise southern species *Pupilla australis* (Figure 23) is known from a single record at Point Quobba, north of Carnarvon. *Gastrocopta* is represented by a few species. Several records are known for the "Red Centre" species *G. deserti* (Figures 9, 14, 15); and two endemic species, *G. wallabyensis* and *G. pilbarana* (Figures 13–15), have limited records, with occasional microsympatry. Much more collecting is needed in this region.

The "Red Centre" has a slightly more extensive radiation, showing a mixture of very common and widely distributed species (*Gastrocopta deserti,* Figure 7; *Pupoides beltianus,* Figure 25; *P. eremicolus,* Figure 26), widely distributed, but clearly disjunct taxa (*G. tatei,* Figures 11, 12; *G. larapinta,* Figure 11), and two species of very limited "Red Centre" distribution (*Pupilla ficulnea,* Figure 21; *Pupoides ischnus,* Figures 12, 21).

All of the species have been collected from stream drift or fig litter near Glen Helen (WA-113), MacDonnell Ranges, and in Palm Valley (WA-130, WA-131), Krichauff Ranges. All of these localities lie in the Finke River drainage. The relative abundance of the three species of *Gastrocopta* varies greatly from locality to locality (SOLEM, 1989:490). Once the wetter mountains are left, the number of microsympatric species declines. *Pupilla ficulnea* and *Pupoides ischnus* are restricted to the central area (Figure 21). The dextral species *Pupoides beltianus* (Figure 25) is common from the Jervois Range, northeast of Alice Springs, to the Barrow Range in Western Australia, with a probable extension to the Shark Bay area (Figure 29). The sinistral *Pupoides eremicolus* (Figure 26) has been collected at Boulia, Black Mt., and Saxby Downs Homestead in western Queensland, then from Tennant Creek and the Dulcie Range through the Krichauff Ranges; it has not been collected in Western Australia. *Gastrocopta deserti* (Figure 7) has a significant set of western Queensland records, inhabits northern parts of the Flinders Ranges, where it has one microsympatric record with *G. margaretae* (Figure 8), is common in the Everard and Mann Ranges (Figure 8), reaches the south fringes of the Kimberley, and near Katherine in the Northern Territory (Figure 10), and then the west coast between Point Quobba and Dampierland (Figures 9, 14, 15). *Gastrocopta tatei* (Figure 11) partly overlaps the range of *G. larapinta* in the "Red Centre," but extends farther west and has an isolated

Table 5

Species diversity in Kimberley wet areas.

	Island samples		Coastal samples		Inland samples	
Number of species	Number	Percent	Number	Percent	Number	Percent
0	10	11.0	0	0.0	2	6.5
1	20	22.0	2	5.7	2	6.5
2	14	15.4	2	5.7	3	9.7
3	18	19.8	11	31.4	4	12.9
4	14	15.4	12	34.5	8	25.8
5	10	11.0	6	17.1	8	25.8
6	5	5.5	1	2.9	4	12.9
7	0	0.0	1	2.9	0	0.0
TOTALS	91	100.1	35	100.0	31	100.0
Mean number of species/sample	2.62		3.74		3.74	

record near Elsey Falls, Roper River, "Top End." *Gastrocopta larapinta* extends farther east into the Dulcie and Jervois Ranges (Figure 11) and then appears in Brooking Gorge, Oscar Ranges, Western Australia, plus a more northern locality, the Carson Escarpment.

Thus, only two species, *Pupoides ischnus* and *Pupilla ficulnea,* are restricted to the "Red Centre." The other five show varying patterns of presence in other parts of Australia.

In wetter refugia of the "Red Centre," most pupilloid species can be found in the litter under a single small patch of figs.

The Kimberley and "Top End" have the largest number of species and the most complex patterns of local diversity. A basic area differentiation must be made on moisture patterns. The Darwin to Gulf of Carpentaria part of the "Top End" and the Prince Regent River to Kalumburu part of the northwest Kimberley have 1000–1500 mm wet seasons. The area near Katherine, Northern Territory, the area along the border from Sir Joseph Bonaparte Gulf inland to Halls Creek, and the chain of Devonian limestone reefs from the Napier Range southeast through the Emanuel and Lawford Ranges have only a 500–759 mm wet season. The two coastal and slightly inland wet regions thus grade into drier and eventually inland desert regions to the south. In addition, they are separated by a trough of land with reduced rainfall that extends along the Western Australia-Northern Territory (WA-NT) border. Each section of this region has its own peculiarities of faunal composition and diversity patterns. Distributional data on the "Top End" sections are based upon several sources: collections made by Vince Kessner, as reported in SOLEM (1989:468–516); collections from the "dry trough of the WA-NT border area" made by the author and reported on in SOLEM (1988:71–74); collections from the limestone fringes of the south Kimberley by A. Solem in 1976–1985 and R. Cameron in 1988; and the Kimberley wet area collections primarily by Vince Kessner during the Rainforest Survey of June 1987 (reported on in SOLEM, in press) and the Kimberley Coast Expedition of June and July 1988 (data summarized here).

Fringe intruders from other regions number seven: *Nesopupa novopommerana* (Figure 3) from near Darwin and the Drysdale River, then Tanimbar Islands and New Britain, Bismarck Archipelago; *Gastrocopta macdonnelli* (Figures 11, 16) from Darwin and Melville Island east to Torres Strait and south at least to Townsville, Queensland; *Gastrocopta deserti, G. tatei,* and *G. larapinta,* all from the "Red Centre" (Figures 10, 11); *Gastrocopta mussoni* (Figures 3, 32), described from near coastal Queensland; and *Glyptopupoides egregia* (Figures 31, 32) from Queensland and northern New South Wales, and then mainly inland parts of the Kimberley wet area.

The wet portion of the "Top End" has a typical assemblage of *Pupisoma orcula, Pupisoma circumlitum, Pumilicopta kessneri, Nesopupa mooreana,* and *Gastrocopta macdonnelli* (near the coast) or *G. simplex* (more inland). Dry inland areas will tend to have *Gastrocopta recondita* (otherwise an Indonesian species), *Pupoides pacificus, G. simplex* (or *G. deserti, G. tatei, etc.*), and (on limestone) *Gyliotrachela catherina,* but will be without some of the wetter area taxa. There thus is a common pattern of three to five microsympatric species.

The zone along the WA-NT border has many limestone hills that, in general, hold large land snail populations. In the wetter northern area of the Ningbing Ranges and Jeremiah Hills, the restricted endemic *Gyliotrachela ningbingia* (Figures 17, 18) and *Gastrocopta simplex* (Figures 7, 10) are nearly ubiquitous (see SOLEM, 1988:90, 94), while *Pupoides pacificus* (Figure 25; SOLEM, 1988:97) is much less common. There are one to three records each for *Pupisoma orcula, Pupisoma* sp., and *Nesopupa mooreana* from swamp adjacent to the Ningbing Ranges. Further inland, there are only records of *Gastrocopta simplex, Pupoides pacificus,* and occasionally *G. deserti* or *G. recondita.* A pattern of two or three microsympatric species is typical.

Along the limestone hills that border the south margin of the Kimberley, there is a clear pattern of gradual reduction in species diversity from the wetter northwest corner (750 mm) to the much drier Lawford Ranges (550 mm). Rainfall records are not adequate to provide correlations, but the general pattern is simple. In the northwest Napiers, *Gastrocopta macrodon* (a wet Kimberley taxon at its southern limit), *G. recondita* (a south fringes species at its northern Australian limit), sometimes *G. simplex* (a dry Kimberley-"Top End" species), *Pupoides pacificus* (a dry zone transcontinental north Australian species), and *Gyliotrachela napierana* (Figures 17, 18; a restricted endemic in the northwest Napier Range) can be present. This gives a four to five microsympatric species pattern. *Gastrocopta macrodon* has a sporadic range, from the Van Emmerick Range to Stumpy's Well, then reappearing about 2–4.7 km south of Yammera Gap, and again near the Lillimilura Police Station ruins. *Gastrocopta recondita* and *Pupoides pacificus* continue throughout the limestone hills, and *Gastrocopta simplex* becomes more abundant to the southeast. *Gyliotrachela napierana* extends southeast to Barker Gorge and then reappears briefly in a highly dissected set of hills about 2.3–2.4 km south of Wombarella Gap and at the "Dingo Caves" some 10.6 km south of Yammera Gap. From here to Brooking Gorge in the Oscar Ranges, the number of pupilloid species is usually only two or three—*Gastrocopta recondita* and/or *G. simplex,* and *Pupoides pacificus.* In Brooking Gorge, there are isolated records for *Gastrocopta larapinta,* and *G. mussoni* has been collected near the Brooking Spring Station air strip, increasing the degree of local diversity. Southeast of the Oscar Range, there are only scattered records for *G. simplex* and *P. pacificus.*

Thus, diversity along the south fringe of the Kimberley shifts from five to two species along a northwest to southeast axis. This correlates with a similar gradient of decrease in wet season rainfall.

The greatest numbers of species and genera, plus the highest levels of local diversity, are found in the wet areas of the northwest Kimberley (see Tables 4, 5). Two comprehensive field surveys provided directly comparable data on local diversity in relation to habitat and area history, permitting observations on local diversity shifts. The Rainforest Survey of June 1987 focused on a broad sampling of vine thicket patches throughout the Kimberley, making 82 stations in 20 field days. Their sampling included very few stations from islands, because the helicopter used in this survey was not equipped with over-water safety equipment. In June and July 1988, a joint Western Australian Museum-Australian Museum-Field Museum of Natural History expedition visited 84 islands off the Kimberley Coast using the chartered vessel *North Star* and made 115 collecting stations. A very few of the stations from the two trips overlapped.

Of the pupilloid species previously collected in the Kimberley and reported on by SOLEM (1989), only *Nesopupa novopommerana,* from inland portions of the Drysdale River National Park, was not obtained by the two survey teams. The only possibly additional species obtained were: (1) a small series of dead *Gastrocopta* from near Kalumburu (SOLEM, in press) that may represent an unknown species or may be subadults of a known species and (2) a recollected, sinistral *Pupoides* from Cassini Island that probably is distinct.

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APPENDIX 1

List of Reviewed Australian Pupilloid Taxa

* Indicates an introduced species.

Genus *Gastrocopta* Wollaston, 1878

(Synonyms: *Australbinula* Pilsbry, 1916; *Gyrodaria* Iredale, 1940;
Papualbinula Iredale, 1941)

Gastrocopta deserti Pilsbry, 1917
Synonym: *helmsiana* Iredale, 1939.
See SOLEM, 1986:102–103, figs. 13–15; SOLEM, 1989: 487–489, figs. 48–53.
Type locality: "Red Centre," Australia.

Gastrocopta larapinta (Tate, 1896)
See SOLEM, 1989:490–491, figs. 54–55.
Type locality: "Red Centre," Australia.

Gastrocopta macdonnelli (Brazier, 1875)
See SOLEM, 1989:492–493, figs. 60–61.
Type locality: Fitzroy Island, NE Queensland.

Gastrocopta macrodon Pilsbry, 1917
See SOLEM, 1989:495–496, figs. 62–67.
Type locality: Milne Bay, Papua, New Guinea.

Gastrocopta margaretae (Cox, 1868)
Synonyms: *bannertonensis* Gabriel, 1930; *complexa* Iredale, 1939.
See SOLEM, 1986:99–101, figs. 1–10.
Type locality: Wallaroo, South Australia.

Gastrocopta mussoni Pilsbry, 1917
See SOLEM, 1989:494, figs. 211–213.
Type locality: Calliungal (= Mt. Morgan), SE Queensland.

**Gastrocopta pediculus* (Shuttleworth, 1852)
See SOLEM, 1989:486–487, figs. 46–47.
Type locality: Marquesas Islands.
Comment: Probably of Indonesian origin.

Gastrocopta pilbarana Solem, 1986
See SOLEM, 1986:103–104, figs. 16–20.
Type locality: Sandy Point, Dirk Hartog Island, Shark Bay, Western Australia.

Gastrocopta recondita (Tapparone-Canefri, 1883)
Synonym: *niobe* Fulton, 1899.
See SOLEM, 1989:496–497, figs. 73–78.
Type locality: Wokan, Aru Islands.

**Gastrocopta servilis* (Gould, 1843)
Synonyms: *microsoma* Tapparone-Canefri, 1883: *lyonsiana* Ancey, 1892.
See SOLEM, 1989:483–484, figs. 38–41.
Type locality: near Matanzas, Cuba.
Comment: Of West Indian origin, introduced on plants.

Gastrocopta simplex Solem, 1989
See SOLEM, 1989:484–486, figs. 42–45.
Type locality: Pentecost River, El Questro Homestead, SW of Wyndham, Western Australia.

Gastrocopta tatei Pilsbry, 1917
See SOLEM, 1989:491–492, figs. 56–59.
Type locality: Central Australia.

Gastrocopta wallabyensis (E. A. Smith, 1894)
See SOLEM, 1986:101–102, figs. 11–12.
Type locality: E Wallaby Island, Houtman Abrolhos group, Western Australia.

Genus *Glyptopupoides* Pilsbry, 1926
(Synonym: *Famarinia* Iredale, 1933)

Glyptopupoides egregia (Hedley & Musson, 1891)
Synonym: *hedleyi* Pilsbry, 1926.
See SOLEM, 1989:506–508, figs. 214–217.
Type locality: Calliungal (= Mt. Morgan), Queensland.

Genus *Gyliotrachela* Tomlin, 1930
(Synonyms: *Gyliauchen* Pilsbry, 1917 [*non* Nicoll, 1915]; *Gyliotrachela* Pilsbry, 1931)

Gyliotrachela australis (Odhner, 1917)
See SOLEM, 1981:92, figs. 7, 8, 12.
Type locality: Chillagoe Caves, N Queensland.

Gyliotrachela catherina Solem, 1981
See SOLEM, 1981:91–92, figs. 5, 6, 11, 17; SOLEM, 1989: 504–505, figs. 97–102.
Type locality: 19 km S of Katherine, Northern Territory.

Gyliotrachela napierana Solem, 1981
See SOLEM, 1981:91, figs. 3, 4, 10, 14–16, 18, 19; SOLEM, 1989:503–504, figs. 94–96.
Type locality: 5.7 km N of No. 8 Bore, Ningbing Ranges, N of Kununurra, Western Australia.

Genus *Nesopupa* Pilsbry, 1900
(Synonym: *Westralcopta* Iredale, 1939)

Nesopupa mooreana (E. A. Smith, 1894)
See SOLEM, 1989:477–479, figs. 33–37.
Type locality: Roebuck Bay, Western Australia.

Nesopupa novopommerana I. Rensch, 1932
Synonym: *tenimberica* Haas, 1937.
See SOLEM, 1989:476–477, figs. 27–32.
Type locality: Karlei, Weite Bucht, Neu-Pommerm (= New Britain), Bismarck Archipelago.

Genus *Pumilicopta* Solem, 1989

Pumilicopta bifurcata Solem, 1989
See SOLEM, 1989:497–498, figs. 88–90.
Type locality: Mountain near Bouldercome, central Queensland.

Pumilicopta kessneri Solem, 1989
See SOLEM, 1989:499–500, figs. 85–87.
Type locality: Wunyu Beach, West Arnhem Land, Northern Territory.

Pumilicopta sp.
See SOLEM, 1989:498.
Locality: Westgid Creek, Bellenden Ker Range, northeast Queensland.

Genus *Pupilla* Leach, 1828
(Synonym: *Omegapilla* Iredale, 1937)

Pupilla (*Gibbulinopsis*) *australis* (Adams & Angas, 1864)
Synonyms: *lincolniensis* Cox, 1867; *occidentalis* Iredale, 1939.
See SOLEM, 1986:105–107, figs. 21–24.
Type locality: Fleurieu Peninsula, South Australia.

Pupilla (*Gibbulinopsis*) *ficulnea* (Tate, 1894)
See SOLEM, 1989:505–506, figs. 103–104.
Type locality: Central Australia.

Genus *Pupisoma* Stoliczka, 1873
(Synonym: *Imputegula* Iredale, 1937)

Pupisoma circumlitum Hedley, 1897
See SOLEM, 1989:473–474, figs. 17, 24, 25.
Type locality: Bundaberg, Queensland.

Pupisoma orcula (Benson, 1850)
See SOLEM, 1989:472–473, figs. 18, 21–23.
Type locality: Between Jounpore and Benares, India.

Pupisoma sp.
See SOLEM, 1989:475, figs. 16, 26.
Locality: Scattered Northern Territory records and Ningbing Ranges, Western Australia.

Genus *Pupoides* Pfeiffer, 1854
(Synonymy: *Themapupa* Iredale, 1930)

Pupoides adelaidae (Adams & Angas, 1864)
Synonyms: *ramsayi* Cox, 1864; *asserta* Iredale, 1939; *contexta* Iredale, 1939; *amolita* Iredale, 1940.
See SOLEM, 1986:111–113, fig. 31.
Type locality: South Australia.

Pupoides aff. *adelaidae* (Adams & Angas, 1864)
See SOLEM, 1986:114–115, figs. 32–33.
Locality: Shark Bay and slightly north, Western Australia.

Pupoides beltianus (Tate, 1894)
See SOLEM, 1989:511–513, fig. 107.
Type locality: Central Australia.

Pupoides aff. *beltianus* (Tate, 1894)
See SOLEM, 1986:114, fig. 36.
Locality: Shark Bay to North West Cape and Hamersley Range, Western Australia.

Pupoides contrarius (E. A. Smith, 1894)
See SOLEM, 1986:109–111, figs. 27, 28.
Type locality: East Wallaby Island, Houtman Abrolhos, Western Australia.

Pupoides eremicolus (Tate, 1894)
See SOLEM, 1989:509–511, fig. 106.
Type locality: Central Australia.

Pupoides ischnus (Tate, 1894)
Synonym: *latior* Iredale, 1937.
See SOLEM, 1989:508–509, fig. 105.
Type locality: Central Australia.

Pupoides lepidulus (Adams & Angas, 1864)
See SOLEM, 1986:113–114, fig. 34.
Type locality: Shark Bay, Western Australia.

Pupoides myoporinae (Tate, 1880)
Synonym: *sinistrorsus* Tate, 1879 [*non* Serres, 1841].
See SOLEM, 1986:108–109, figs. 25, 26.
Type locality: Peelunbie, Head of the (Great Australian) Bight, South Australia.

Pupoides pacificus (Pfeiffer, 1846)
Synonyms: *anapacifica* Iredale, 1939; *dirupta* Iredale, 1939; *comperta* Iredale, 1940.
See SOLEM, 1989:513–516, figs. 108–114.
Type locality: Sir Charles Hardy's Island, Cape York Peninsula, Queensland.

List of Unrevised Pupilloid Taxa

The following taxa listed in the nomenclatural checklist of IREDALE (1937a:301–306) have not been reviewed for lack of adequate material. It is possible neither to characterize them adequately as species nor to delineate meaningful distributional ranges. References are given both to IREDALE (1937a) and the early revisions by PILSBRY (1916–1918, 1920–1921). Comments are given where appropriate.

Gastrocopta hedleyi Pilsbry, 1917
See PILSBRY, 1916–1918:166–167, pl. 27, figs. 1–4; IREDALE, 1937a:301.
Type locality: Narrabri, New South Wales.
Comment: A dextral shell with a huge, slanted columellar barrier whose anterior end is lower; parietal long and crescentic; basal tiny and tubercular; lower palatal strongly angled.

Gastrocopta macleayi (Brazier, 1876)
See PILSBRY, 1916–1918:162–164, pl. 27, fig. 9; IREDALE, 1937a:302.
Type locality: Bet and Sue Islands, Torres Strait, Queensland.
Comment: Probably a synonym of *G. macdonnelli* (Brazier, 1875).

Gastrocopta moretonensis (Cox, 1868)
See PILSBRY, 1916–1918:161–162, pl. 26, figs. 12, 13; IREDALE, 1937a:301.
Type locality: Moreton Bay, Queensland.
Comment: Type specimens probably lost, no topotypes seen; original illustration inadequate for identification purposes.

Gastrocopta queenslandica Pilsbry, 1917
See PILSBRY, 1916–1918:159–160, pl. 26, fig. 2; IREDALE, 1937a:301.
Type locality: Calliungal (= Mt. Morgan), Queensland.
Comment: The type illustration looks like a "new adult" of *G. pediculus* (Shuttleworth, 1852) in which the apertural barriers are still undersized.

Gastrocopta rossiteri (Brazier, 1875)
See PILSBRY, 1916–1918:147; IREDALE, 1937a:302.
Type locality: Picton, New South Wales.
Comment: Probably based upon examples of *G. pediculus* (Shuttleworth, 1852).

Gastrocopta strangeana Iredale, 1937
Synonym: *strangei* Pfeiffer, 1854, *non* Benson, 1853.
See PILSBRY, 1916–1918:157–158, pl. 26, figs. 3–6; IREDALE, 1937a:301.
Type locality: Gordon (= Garden) Island, Port Jackson, New South Wales.
Comment: A sinistral shell with the parietal and angular barriers well separated; columellar barrier simple and not inclined; basal a tiny knob; lower palatal crescentic; upper palatal a medium-sized knob. The only sinistral Australian *Gastrocopta*. IREDALE (1940:234) proposed a new genus, *Gyrodaria,* for this species.

Gastrocopta strangeana trita (Iredale, 1940)
See IREDALE, 1940:233–234, fig. 3.
Type locality: Narrabri, New South Wales.
Comment: A "larger sinistral form" of *G. strangeana* is the only differentiating phrase. Probably a *nomen nudum.*

Genus *Cylindrovertilla* Boettger, 1880
(Synonym: *Wallivertilla* Iredale, 1937)

Comment: Minute, sinistral shells, recorded from New Caledonia and the Queensland-New South Wales arc; mainly coastal areas. Parietal barrier has been lost, but a prominent angular barrier remains.

Cylindrovertilla fabreana boynensis Iredale, 1937
See PILSBRY, 1916–1918:47–48, pl. 5, figs. 12, 13; IREDALE, 1937a:303.
Type locality: Boyne Island, Port Curtis, Queensland.

Cylindrovertilla hedleyi Pilsbry, 1920
See PILSBRY, 1920–1921:46, pl. 5, figs. 4, 10; IREDALE, 1937a:303.
Type locality: Calliungal (= Mt. Morgan), Queensland.
Comment: Lower palatal barrier lost, others reduced in size.

Cylindrovertilla kingi (Cox, 1864)
See PILSBRY, 1920–1921:44–46, pl. 5, figs. 1–3; IREDALE, 1937a:303.
Type locality: Paramatta, New South Wales.
Comment: Two palatal barriers present.

Cylindrovertilla kingi negata Iredale, 1940
See IREDALE, 1940:233, 235, fig. 2.
Type locality: Tweed River, New South Wales.
Comment: Probably a synonym of *C. kingi* (Cox, 1864).

Pupilla nelsoni (Cox, 1864)
See PILSBRY, 1920–1921:219–220—as synonym of *P. australis* [Adams & Angas, 1864]; also see IREDALE, 1937a:304.
Type locality: Nelson's Bay, Sydney, New South Wales.
Comment: Probably a synonym of *P. australis.*

Pupilla tasmanica (Johnston, 1883)
See PILSBRY, 1920–1921:219–221, pl. 23, fig. 18—as synonym of *P. australis* [Adams & Angas, 1864]; also see IREDALE, 1937a:305.
Type locality: Tasmania.
Comment: Probably a synonym of *P. australis.*

Genus *Somniopupa* Iredale, 1937

Comment: Quite probably a *nomen nudum.*

Somniopupa scotti Brazier, 1875
See PILSBRY, 1920–1921:222, pl. 23, fig. 22; IREDALE, 1937a:305.
Type locality: Fitzroy Island, Queensland.
Comment; Based on a single, probably juvenile example. Very probably a synonym, but its identity remains uncertain.

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